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A Turonian bivalve pearl from Russia and a review of Cretaceous pearl records

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A fossil bivalve pearl is reported for the first time from Cretaceous deposits of Russia. The specimen originates from Turonian strata of the Voronezh Region and was produced by inoceramid bivalves, either *Inoceramus* ex gr. *inaequivalvis* Schlüter, 1877 or *I. stuemckei* Heinz, 1928. High-resolution micro-computed tomography was used to investigate the internal structure of the pearl, allowing reconstruction of its growth history and demonstrating that it represents a blister pearl with a nucleus that became detached from the shell. This study constitutes the first application of high-resolution micro-CT to a pre-Quaternary fossil bivalve pearl. A review of all 24 known Cretaceous localities yielding fossil pearls is presented, of which 21 are Late Cretaceous in age, documenting a pronounced Late Cretaceous peak in pearl occurrences. A possible explanation for this pattern is proposed. The Late Cretaceous diversification of large inoceramid bivalves with hypertrophied calcitic prismatic shell layers favoured the formation of predominantly calcitic pearls, which have a substantially higher preservation potential than aragonitic pearls. Analysis of Mesozoic and Paleogene pearl occurrences indicates that interpretations of pearl formation in deep time are strongly shaped by preservational bias. Pearls composed mainly of calcite and produced by bivalves with thick calcitic shells are far more likely to be preserved, resulting in a fossil record strongly biased towards calcitic pearl producers. These results demonstrate that preservational bias strongly structures the fossil record of pearls and likely obscures the true diversity of pearl-producing bivalves through geological time. □ *Fossil pearl, inoceramid bivalves, Turonian, Voronezh Region, micro-computed tomography, palaeopathology.*

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Bivalve pearls are biogenic objects, the mechanism of whose formation is well understood. Pearls form as a result of damage to the mantle, which leads to the displacement of mantle epithelial cells into the connective tissue. Subsequent cell division results in the formation of a closed cyst, known as a pearl sac (Taylor & Strack 2008; Hänni 2012). Damage to the mantle may be caused by a variety of factors, including predator attacks, the activity of parasites within the mantle tissue, the intrusion of foreign particles (sand grains, small pebbles, shell fragments, etc.), storm-related mechanical stress, or even products of the mollusc's own metabolism (Taylor & Strack 2008).

Pearls that, during free growth, come into contact with the shell and become attached to it are referred to as blister pearls. This type of pearl is most commonly encountered in the fossil record owing to its direct association with the shell of the producing organism. However, many free pearls in the fossil record have probably been overlooked or misidentified, especially when already incorporated into the sediment.

In some cases, blister pearls may be confused with blisters. Blisters are not pearls, as they represent irregularities on the inner shell surface formed by the overgrowth of a foreign object or a parasite (Stevens *et al.* 2020). In most, though not all, cases blisters have an irregular shape, in contrast to the nearly spherical morphology typical of blister pearls (Taylor & Strack 2008). Reliable discrimination between these structures requires investigation of their internal structure, which can be achieved through the preparation of thin sections and polished surfaces or by means of computed tomography (Hoffmann *et al.* 2020; Stevens *et al.* 2020). The latter method is preferable because it is non-destructive.

Numerous studies, including many recent ones, have been devoted to the problem of pearl formation. This sustained interest is largely explained by the long-standing use of pearls in jewellery over many centuries. It is evident that the mechanism of pearl formation in the geological past was the same as that observed today. Consequently, pearl occurrences might be expected throughout the Phanerozoic, beginning with the appearance of bivalve molluscs in the Cambrian. Nevertheless, fossil pearls are relatively rare, which allows them to be regarded as a unique type of fossil.

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Thus, fossil pearls represent a distinct palaeontological problem. Despite their mineral nature and the relatively simple mechanism of their formation, pearls are rarely encountered in the fossil record. Moreover, their occurrences are unevenly distributed throughout the Phanerozoic.

Palaeozoic pearls are known only from Silurian localities with silicified faunas on the island of Gotland, Sweden, and in the Czech Republic (Kříž 1979; Liljedahl 1985, 1994). The apparent absence of pearl finds from other Palaeozoic silicified faunas has previously been noted as enigmatic (Kauffman 1990). Triassic pearls have been recorded from two localities in Germany: the oldest known free pearl from Upper Triassic deposits (Kutassy 1937) and an imprint on a shell valve, apparently left by a detached blister pearl, from the Middle Triassic (Geyer *et al.* 2005, fig. 3R). Pearls of Jurassic age are known from nine localities (Deshayes 1831; Morris 1851; Inostrantsev 1898; Jackson 1909; Dorn 1937; Kolesnikov 1974; Gerasimov 1984).

The vast majority of known Jurassic pearls were produced by oysters. The most prolific occurrences of fossil pearls are associated with the Cretaceous System. More than 20 Cretaceous localities yielding bivalve pearls have been documented, the overwhelming majority of which are attributed to inoceramids (Boucot & Poinar 2010). Considerably fewer pearls are known from Palaeogene deposits than from the Upper Cretaceous (Zilch 1936). In Neogene deposits, pearls occur relatively regularly (Okumura & Karasawa 1994; Binder 2015; Khalili & Vinn 2023). However, even from Pleistocene deposits, fewer than ten localities yielding fossil pearls have been reported (Karasawa *et al.* 2013; Li *et al.* 2016).

Fossil pearls have been studied far less extensively than their modern counterparts. In most publications on this topic, authors have limited their observations to reporting the occurrence of pearls, without addressing their internal structure or formation mechanisms. For a long time, investigation of pearl internal structure was possible only through destructive methods. In the present study, we apply micro-computed tomography combined with three-dimensional model visualization to fossil pearls of bivalves for the first time. Previously, a similar approach was applied to the study of a blister pearl in a belemnite (Stevens *et al.* 2020).

Material and methods

Material, locality and stratigraphical context

The material originates from a section of Turonian deposits exposed near the village of Losevo, Voronezh Region, approximately 110 km south-west of Voronezh, Russia (Fig. 1). The section represents marine chalk deposits typical of the epicontinental seas of the Russian Platform (Walaszczyk *et al.* 2004; Kopaevich *et al.* 2025). Fossils from the Cretaceous strata of this section have been collected in situ from stratigraphically constrained horizons by a local amateur palaeontologist for more than 10 years. During this period, a large and representative collection of fossil fauna has been assembled; however, only a single isolated specimen of fossil pearl has been recovered.

In addition to the fossil pearl, the section yields massive calcitic hinges (Fig. 2C, D) and numerous shell fragments of *Inoceramus*, represented by a thick prismatic shell layer. One such fragment, 7 mm thick, bears an irregularly shaped blister measuring 7 × 4 mm (Fig. $2E_{1-3}$).

Complete inoceramid shells are rare at the Losevo section. All identifiable specimens belong to *Inoceramus* ex gr. *inaequivalvis* Schlüter, 1877 and *Inoceramus stuemckei* Heinz, 1928 (Fig. 2A, B). The presence of the latter species constrains the age of the deposits to the lower part of the Upper Turonian Substage, as this taxon is well documented from coeval strata of Europe and North America (Niebuhr & Wilmsen 2023).

Imaging and analytical methods

Specimen photography was carried out using a TESCAN VEGA 3 scanning electron microscope without coating, and a Leica M165C stereomicroscope equipped with a Flexacam digital camera using Leica LAS X software at the Borissiak Paleontological Institute, Russian Academy of Sciences (PIN RAS, Moscow, Russia). Additional photographs were taken using a medium-format mirrorless digital camera Fujifilm GFX 50R equipped with a Fujinon GF 120 mm F4 R LM OIS WR macro lens at the Geological Institute, Russian Academy of Sciences (GIN RAS, Moscow, Russia).

Only non-destructive analytical methods were applied, as only a single specimen of fossil pearl was available. Micro-CT was performed using a Neoscan 80 micro-CT scanner (Neoscan, Belgium) at PIN RAS. Scanning was conducted using X-ray radiation with a source voltage of 84 kV and a source current of 48 μA, yielding an isotropic voxel size of 4 μm and resulting in a dataset of 1.85 GB. Three-dimensional visualization and further processing, including the generation of virtual sections, specimen measurements and analysis of X-ray attenuation variations, were carried out using CTvox software (64-bit).

Repository

The studied material is housed in the V.I. Vernadsky State Geological Museum of the Russian Academy of Sciences (SGM RAS, Moscow), collection no. SGM-2185.

Definition of pearl-bearing localities

To analyse the taxonomic composition of Cretaceous pearl producers, a compilation of pearl-bearing localities was assembled. Pearl specimens occurring within the same geological formation and stratigraphical stage were treated as originating from a single locality, unless different taxonomic affiliations of the producing organisms could be demonstrated.

Results

The studied pearl measures 7 × 6 mm and is nearly spherical in shape, although one surface is slightly flattened (Fig. 3A$_1$). The pearl is assigned to the blister type but was found isolated from the shell. The flattened surface represents the former attachment area to the shell. The nacreous layer is not preserved, which is typical of Cretaceous fossil pearls (Everhart 2017).

Micro-CT allowed investigation of the internal structure of the pearl. Both fractures of the outer layer, the pearl surface, and CT sections show that the external part of the pearl is composed of a thick prismatic layer (Figs 3–5), a diagnostic feature of Upper Cretaceous inoceramids. The inner part of the pearl displays a predominantly concentric structure. The boundary between the outer and inner parts is clearly visible in the CT sections (Fig. 3D). This boundary most likely separates the predominantly concentric portion formed during the free-growing pearl stage from the radial portion corresponding to the blister pearl stage. The diameter of the inner part ranges from 4.9 to 5.7 mm, whereas the thickness of the outer layer varies from 0.4 to 1.5 mm.

Numerous voids are observed in the CT sections, probably representing spaces left after the decay of

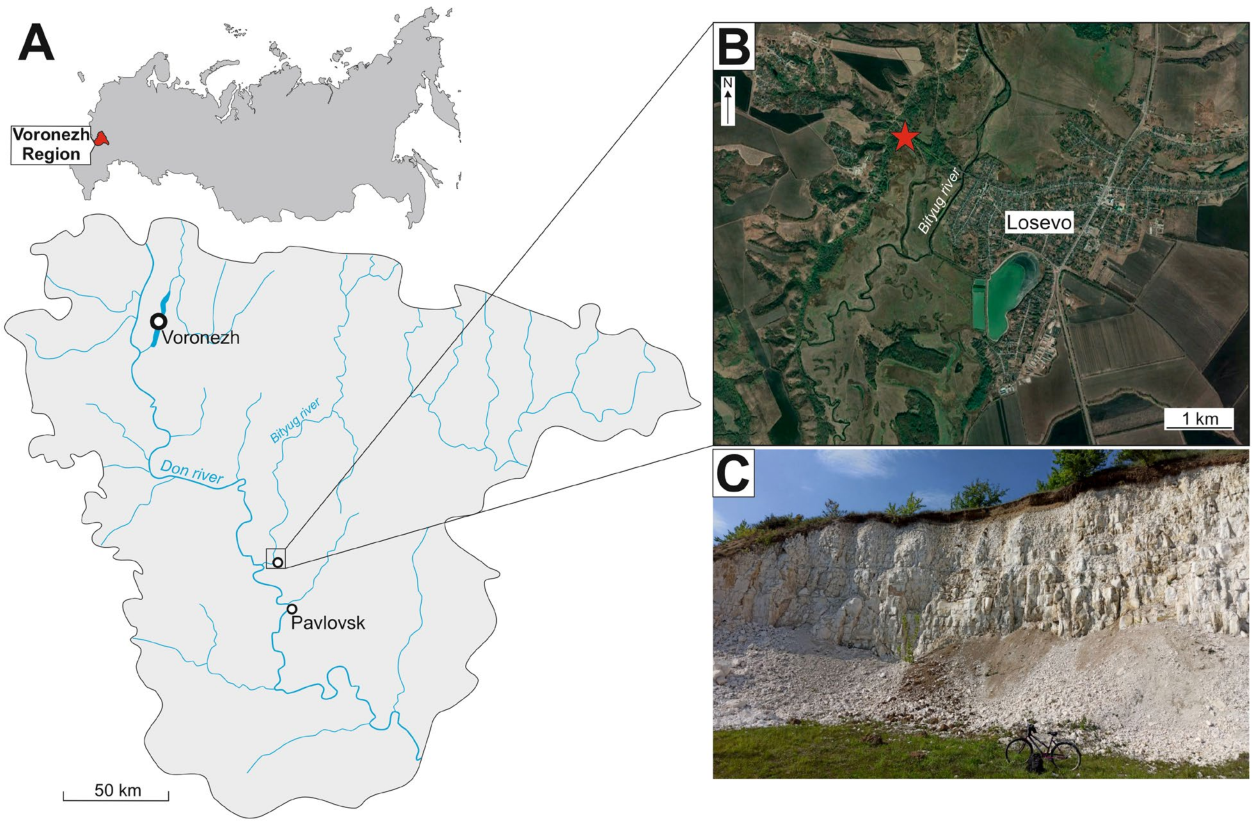

Fig. 1. Location of the Losevo section (Turonian Stage, Voronezh Region, Russia). A, general map showing the geographic position of the study area within the Voronezh Region. B, surroundings of the village of Losevo, C, field photograph of the Turonian outcrop near the village of Losevo (50.684873° N, 40.002643° E); bicycle for scale.

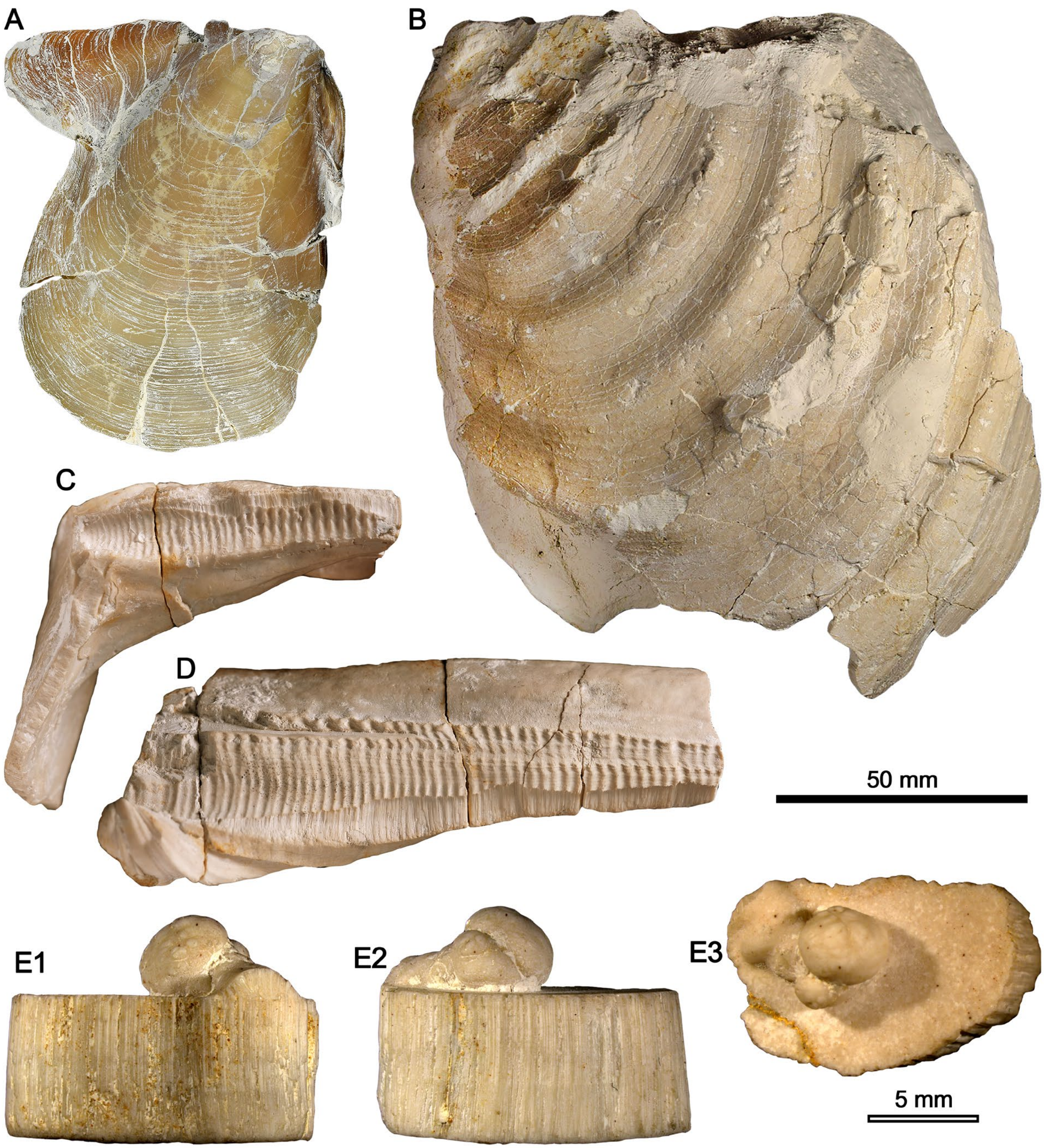

Fig. 2. Preservation of *Inoceramus* shells with massive calcitic hinges and associated blister. A, *Inoceramus* ex gr. *inaequivalvis* Schlüter, 1877. B, *Inoceramus stuemckei* Heinz, 1928. C, hinge fragment. D, fragment of a massive hinge. $E_{1\text{-}3}$, blister on a shell fragment of *Inoceramus*. Black scale bar for A-D, white scale bar for $E_{1\text{-}3}$.

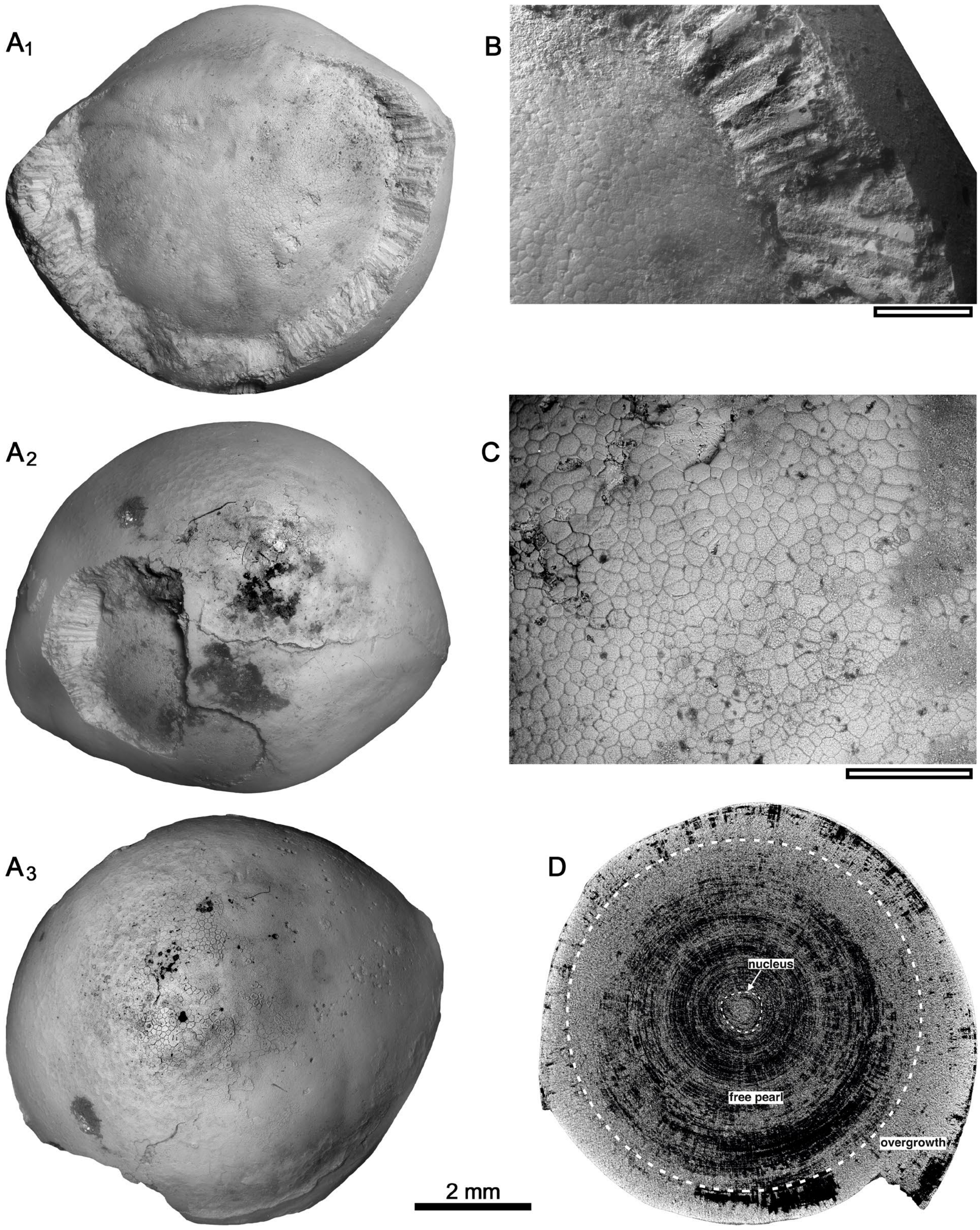

Fig. 3. Fossil inoceramid blister pearl from the Voronezh Region (Upper Turonian, *Inoceramus stuemckei* Zone). A_{1-3}, blister pearl (SEM images). B, C, prismatic layer forming the outer layer of the pearl (SEM images). D, virtual CT section through the centre of the blister pearl. White scale bar, 0.5 mm.

organic matter (Figs 3D, 5). A high organic content is a characteristic feature of pearls (Taylor & Strack 2008) and is considered one of the main reasons for their rare occurrence in the fossil record. The number of voids decreases sharply in the outer part of the pearl, where the material is more homogeneous. This observation further supports the interpretation that the outer portion corresponds to the blister stage, when the free pearl reached the shell and began to accrete to it. A series of successive CT sections documents the formation of the blister pearl by overgrowth of the free pearl by shell material (Fig. 5).

The distribution of X-ray attenuation in the CT section reveals the presence of a nucleus (Fig. 4). It is expressed as a density heterogeneity, denser than the surrounding layers, with a rounded triangular shape and a size of approximately 0.6 mm. Pearls may form either with or without a nucleus. The presence or absence of a nucleus can be reliably established using tomography, as demonstrated for modern pearls (Krzemnicki *et al.* 2010; Otter *et al.* 2014). In the studied specimen, the presence of an angular nucleus is clearly demonstrated. The nucleus may represent a shell fragment that entered the mantle cavity and caused damage to the mantle epithelium. Previously, the presence of a nucleus in fossil pearls based on tomographic data had been documented only for a Pleistocene specimen from China (Li *et al.* 2016).

Although the pearl was found isolated from the shell, it can be confidently attributed to inoceramids. Indirect evidence for the role of inoceramids as pearl producers is provided by the abundance of inoceramid shell fragments in the studied section. A blister was observed on one such fragment (Fig. $2E_{1-3}$). Thus, the producer of the pearl was most likely one of the two inoceramid species recorded from the section, *Inoceramus* ex gr. *inaequivalvis* Schlüter, 1877 or *I. stuemckei* Heinz, 1928. Pearl production has not previously been reported for either of these species.

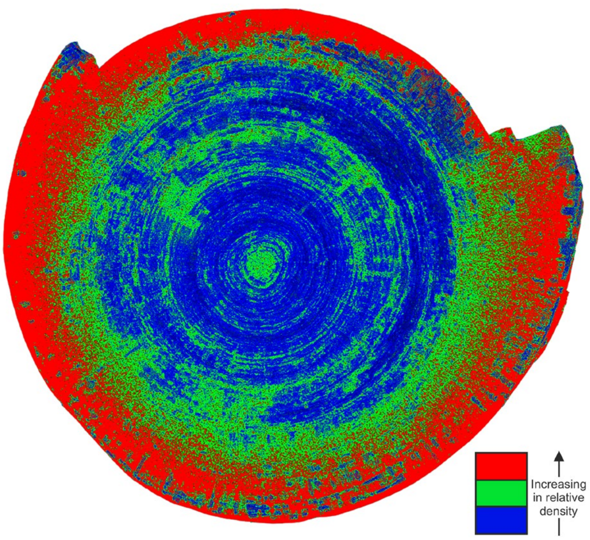

Fig. 4. Colour-coded distribution of X-ray attenuation in a virtual micro-CT section through the centre of the inoceramid blister pearl. Colours indicate relative changes in density.

Cretaceous pearls

More than 20 localities yielding bivalve pearls have been documented from Cretaceous deposits worldwide (Table 1). Only three of these localities are of Early Cretaceous age, all Albian. The vast majority of Cretaceous pearls were produced by inoceramids, whereas in only six cases pearls were secreted by other bivalves. In addition to inoceramids, oysters also acted as pearl producers during the Cretaceous.

Blister pearls produced by the oyster *Exogyra texana* Roemer, 1849 are known from Albian deposits of Texas (Adkins & Winton 1919). More recently, blister pearls from Cenomanian deposits of Portugal have been recorded on shells of *Exogyra (Costagyra) olisiponensis* (Sharpe, 1850) (Carvalho & Fraústo 2020). In the Netherlands, a silicified Late Cretaceous pebble bearing a blister pearl on the shell of *Pycnodonte vesicularis* (Lamarck, 1806) was found in Pleistocene deposits (Anderson 1946). In addition to oysters, Cenomanian blister pearls have been reported from shells of *Isognomon seeleyi* from England (Seeley 1861; Newton 1908; Zilch 1936). Rudist pearls have also been mentioned (Klinghart 1922, *in* Kirchner 1927), although the precise locality and age of this record remain unknown. The only Cretaceous pearls known from continental deposits originate from Albian strata of Mongolia (Kolesnikov 1972, 1973a, 1973b), where they were found enclosed within shells of *Plicatotrigonioides dushiulensis* Martinson & Kolesnikov, 1973 and *Sainshandia* sp.

Inoceramid pearls are by far the most frequently recorded worldwide. Pearl-producing inoceramids include representatives of the genera *Inoceramus*, *Mytiloides*, *Platyceramus*, *Volviceramus*, *Cataceramus* and *Cladoceramus*. The richest locality for fossil pearls currently known is the Upper Coniacian–Lower Campanian Smoky Hill Chalk Member of Kansas (Brown 1940; Kauffman 1990; Everhart 2005, 2017). This unit has yielded several dozen inoceramid pearls, including the largest known fossil pearl, measuring approximately 11 cm in height and 6.5 cm in length (Kauffman 1990, p. 67, fig. 51D, E). In the USA, inoceramid pearls are also known from Turonian and

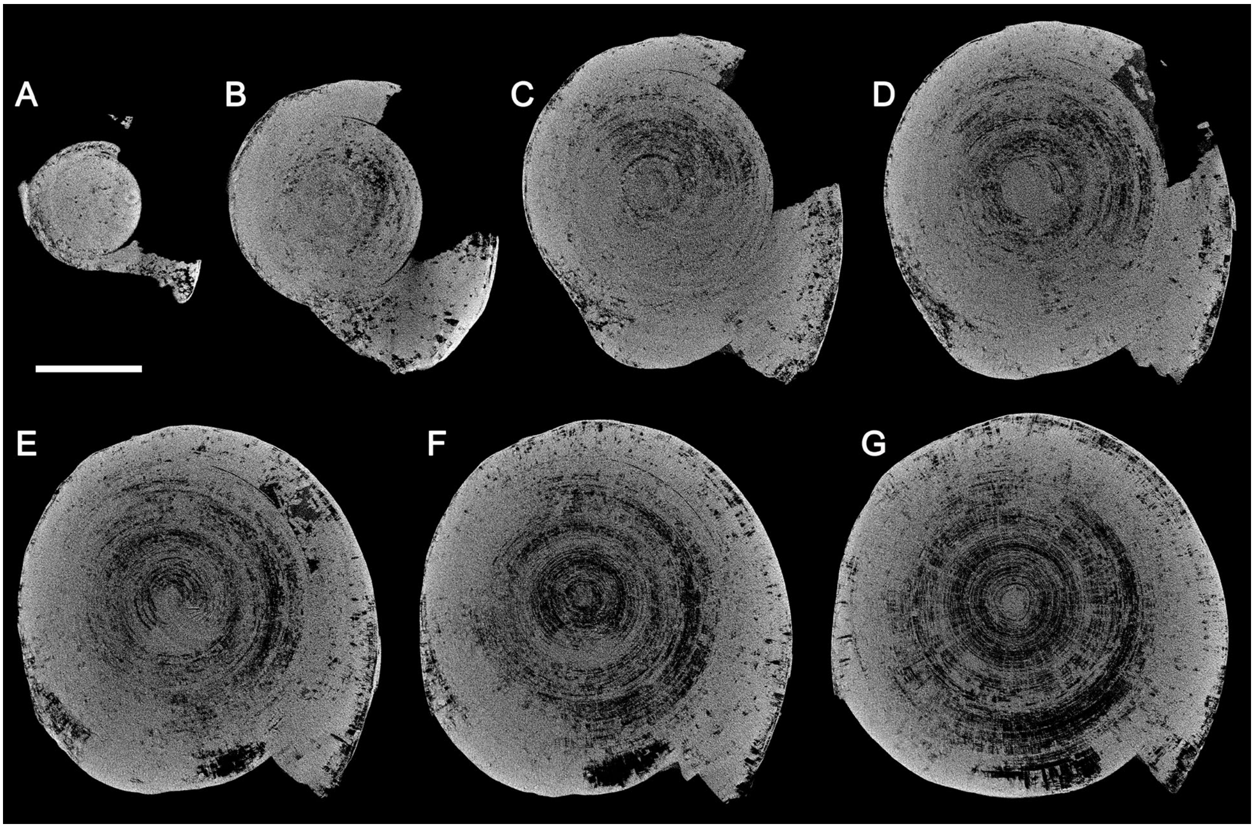

Fig. 5. A-G, sequential virtual micro-CT sections of the blister pearl from the outer surface towards the centre. Scale bar is 2 mm.

Table 1. Localities of Cretaceous bivalve pearls

№	Producer	Locality	Age	Reference
1	*Exogyra texana* Roemer, 1849	Coke County, Texas, USA	Albian	Adkins & Winton 1919, not figured
2	*Plicatotrigonioides dushiulensis* Martinson et Kolesnikov, 1973	Dushi-Ula, Gobi Desert, Mongolia	Albian	Kolesnikov 1972, p. 101, fig. 1; Kolesnikov 1973a, p. 1195, fig. 1; 1973b, p. 138-139, fig.1, 2
3	*Sainshandia*	Dushi-Ula, Gobi Desert, Mongolia	Albian	Kolesnikov 1972, not figured
4	*Isognomon seeleyi* (Zilch, 1936)	Cambridge, England	Cenomanian	Seeley 1861, p. 121, pl. VI, fig. 6; Newton 1908, p. 137, pl. V, fig. 7
5	Inoceramidae	Cambridge, England	Cenomanian	Jackson 1909, p. 321, pl. XIV, fig. C
6	Inoceramidae	Russell County, Kansas, USA	Cenomanian	Everhart 2005, p. 41, not figured; 2017, p. 56, not figured
7	*Exogyra (Costagyra) olisiponensis* (Sharpe, 1850)	Serra do Funchal, Portugal	Cenomanian	Carvalho & Fraústo 2020, p. 56, fig. 2
8	*Mytiloides labiatus* (Schlotheim, 1813)	Blue Bell Hill, Burham, Kent, England	Turonian	Newton 1908, p. 134, pl. V, fig. 1
9	Inoceramidae	Gove and Logan counties, Kansas, USA	Turonian	Brown 1940, p. 366, fig. 1-6, 12-16, 19, 20
10	*Inoceramus cuvieri* Sowerby, 1814	Dallas County, Texas, USA	Turonian	Kauffman 1990, p. 67, fig.51B
11	*Inoceramus stuemckei* Heinz, 1928 or *I. ex gr. inaequivalvis* Schlüter, 1877	Voronezh oblast, Russia	Turonian	This work

(*Continued*)

Table 1. (Continued)

№	Producer	Locality	Age	Reference
12	Inoceramidae	Trego and Gove counties, Kansas, USA	Coniacian	Everhart 2005, p. 40-41, fig. 3.7-3.8; 2017, p. 56-57, fig. 3.16-3.17
13	*Platyceramus* or *Cladoceramus*	Dallas County, Texas, USA	Santonian	Kauffman 1990, p. 67, fig.51C
14	*Platyceramus platinus* (Logan, 1898)	Kansas, USA	Santonian	Kauffman 1990, p. 67, fig.51A
15	*Volviceramus grandis* (Conrad, 1875)	Kansas, USA	Santonian	Kauffman 1990, p. 67, fig.51D,E; Everhart 2005, p. 40, fig. 3.7
16	*Inoceramus sagensis quadrans* Whitfield, 1885	New Jersey, USA	Campanian	Whitfield 1885, p. 79, pl. XIV, fig. 16; Newton 1908, p. 134, pl. IV, fig. 4
17	*Cataceramus subundatus* (Meek, 1861)	Shasta County, California, USA	Campanian	Russell 1929, p. 418-422, fig. 1, 3-9
18	*Cataceramus goldfussianus* (Orbigny, 1847)	Westphalia, Germany	Campanian	Goldfuss 1836, p. 116, pl. 112, fig. 4d; Newton 1908, p. 132, pl. IV, fig. 1
19	*Inoceramus expansus* Bailey, 1855	Pondoland, South Africa	Campanian	Newton 1908, p. 133, pl. IV, fig. 2, 3
20	Inoceramidae	Near Urakawa, Japan	Late Cretaceous	Yokoyama 1890, p. 175, pl. XVIII, fig. 6
21	*Hippurites*	No locality given	Late Cretaceous	Klinghart 1922, in Kirchner, 1927
22	*Pycnodonte vesicularis* (Lamarck, 1806)	Overijssel, the Netherlands	Late Cretaceous	Anderson 1946, not figured
23	Inoceramidae	Suffolk, England	Late Cretaceous	Jackson 1909, p. 321, pl. XIV, fig. D
24	Inoceramidae	Kent, England	Late Cretaceous	Morris 1851, p. 89, pl. IV, fig. 12-14; Newton 1908, p. 135, pl. IV, fig. 5, pl. V, fig. 2-6

Santonian deposits of Texas, Campanian deposits of California and New Jersey, and Cenomanian deposits of Kansas (Whitfield 1885; Russell 1929; Kauffman 1990; Everhart 2005, 2017). Several fossil pearls have also been reported from the Upper Cretaceous of England (Morris 1851; Jackson 1909; Newton 1908) and Japan (Yokoyama 1890), whereas isolated finds are known from Campanian deposits of Germany (Goldfuss 1836) and South Africa (Newton 1908).

Occurrences of fossil pearls in Mesozoic deposits are rare prior to the Late Cretaceous (Fig. 6B). It is noteworthy that pearls are also less frequent in Paleogene deposits than in the Upper Cretaceous. The pronounced Late Cretaceous peak in pearl occurrence remains poorly explained, although it has been repeatedly documented (Kauffman 1990; Boucot & Poinar 2010; Li *et al.* 2016). Importantly, the abundance of pearl finds should not be directly linked to parasitic activity alone (Littlewood & Donovan 2003; Huntley *et al.* 2021), as pearl formation may be triggered by a variety of biological and physical factors. In addition, this pattern is likely influenced by sampling and collecting biases inherent to the fossil record.

Insight into the Late Cretaceous peak in pearl occurrence can be gained by analysing the taxonomic composition of pearl producers (Fig. 6A). Approximately 80% of Upper Cretaceous pearls were produced by inoceramoids, about 10% by Ostreoidea, and the remaining occurrences by other bivalve groups, including rudists and isognomonids. With the exception of the latter, all these groups are characterised by thick shells composed predominantly of calcite (Fig. 6B). Nearly all known Jurassic pearls were produced by oysters, as were most Palaeogene pearls.

Owing largely to the long tradition of pearl use in jewellery, it is well established that pearls are relatively short-lived owing to their high content of organic matter and water (Taylor & Strack 2008). Consequently, current understanding of pearl formation and the identity of pearl producers in the geological past is strongly influenced by preservational bias. The overwhelming majority of known Jurassic to Palaeogene pearls were produced by bivalves with predominantly calcitic shells, whereas pearls secreted by aragonitic or thin-shelled bivalves are far less likely to be preserved.

During the Middle Jurassic to Cretaceous, the Calcite Sea II interval is recognized, characterized by an increase in marine organisms possessing calcitic skeletons (Hautmann 2006; Porter 2010; Ries 2010). This interval broadly coincides with an increase in fossil pearl occurrences in Jurassic and Cretaceous deposits.

Not all modern pearl-producing bivalves possess thick, calcitic shells. The principal pearl producers

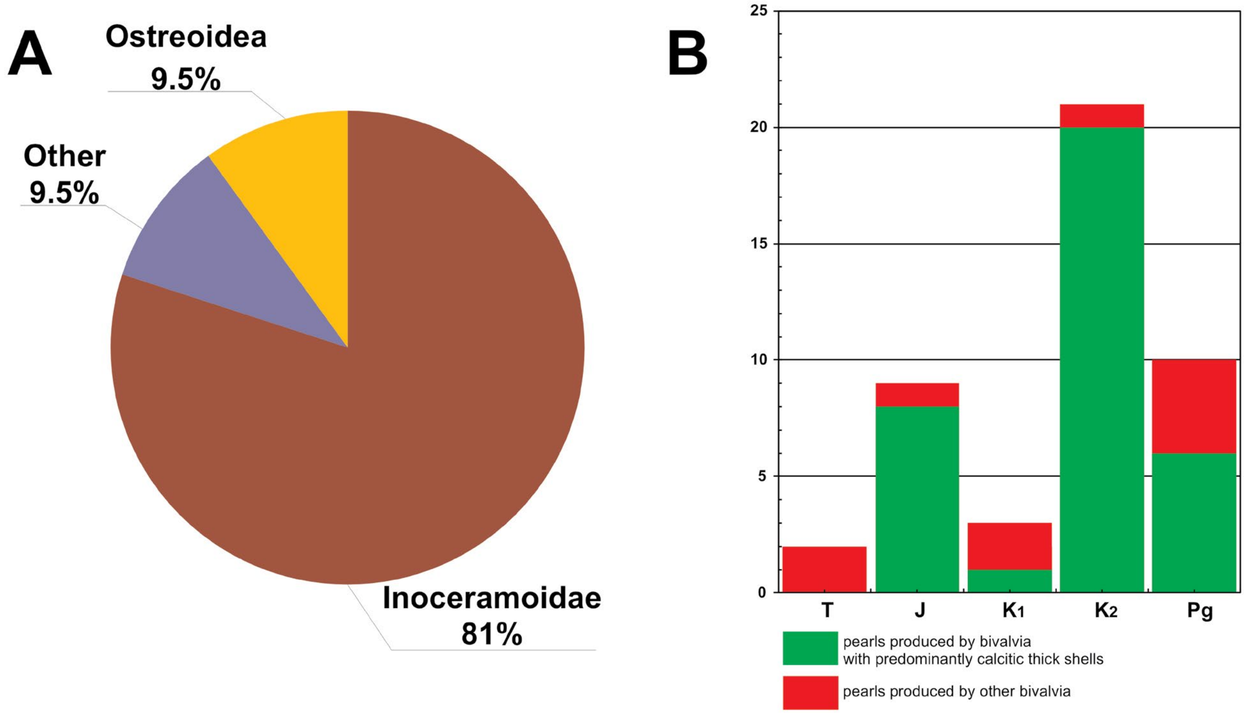

Fig. 6. A, taxonomic composition of pearl-producing bivalves in the Late Cretaceous. B, relative frequency of bivalve pearl occurrences through the Mesozoic and Palaeogene and shell biomineralogy of their producers.

today are species of the genus *Pinctada* in marine environments and representatives of the family Unionidae in freshwater settings. In *Pinctada*, the nacreous layer accounts for more than 60% of the total shell thickness (Strąg *et al.* 2020; Cuif *et al.* 2023), whereas freshwater bivalves typically lack thick shells and calcitic mineralisation. It is therefore plausible that many major pearl producers of the past remain undocumented, and that our current view of pearl formation in the Palaeozoic and Mesozoic is largely governed by selective preservation.

We hypothesise that the sharp increase in pearl occurrences in Upper Cretaceous deposits is related, at least in part, to shell structural characteristics of the producers. The Late Cretaceous radiation of large inoceramids with hypertrophied calcitic prismatic shell layers favoured the formation of pearls composed predominantly of calcite, which is considerably more resistant to diagenetic alteration than aragonite and thus more readily preserved in the fossil record. The inoceramid pearl described herein fits well within this pattern.

This hypothesis also provides a plausible explanation for the scarcity of Palaeozoic pearl finds. During the Palaeozoic, only a limited number of bivalve groups possessed thick, calcitic shells, including certain Permian oyster-like bivalves (Newell & Boyd 1970; Biakov & Mazaev 2023) and the giant Permian Alatoconchidae (Isozaki 2006; Yang *et al.* 2025). All known Palaeozoic pearls derive from exceptional localities with silicified faunas (Kříž 1979; Liljedahl 1985, 1994), where silicification facilitated their preservation in the fossil record.

Conclusion

This study documents the first record of a fossil pearl from Cretaceous deposits of Russia. Previously, fossil pearls of bivalves from Russia were known exclusively from Jurassic strata. The pearl described herein originates from the Upper Turonian deposits of the Voronezh Region.

Scanning electron microscopy reveals that the outer part of the pearl is composed of coarse calcitic prisms, a shell microstructural feature characteristic of inoceramid bivalves. The fossil assemblage of the studied section is dominated by abundant inoceramid shell fragments, including specimens of *Inoceramus* ex gr. *inaequivalvis* Schlüter, 1877 and *I. stuemckei* Heinz, 1928, as well as a blister preserved on an inoceramid shell fragment. One of these species is inferred to have been the pearl producer, although pearl formation has not previously been reported for either taxon.

Although the pearl is preserved isolated from the shell, its morphology and internal structure indicate that it represents a blister pearl. High-resolution micro-CT enabled a detailed reconstruction of its internal structure, including the identification of a nucleus, an inner concentric portion corresponding to a free-growing pearl stage, and an outer radial portion formed during the blister pearl stage. This study represents the first application of high-resolution micro-CT to a pre-Quaternary fossil bivalve pearl, providing new insights into pearl growth in deep time.

A global review of Cretaceous pearl occurrences identifies 24 localities, of which 21 are Late Cretaceous in age, confirming a pronounced Late Cretaceous peak in pearl preservation. The vast majority (95%) of known pearl producers from this interval possessed thick, predominantly calcitic shells, a pattern also observed in Jurassic and, to a lesser extent, Palaeogene records. The increase in fossil pearl occurrences during the Middle Jurassic-Cretaceous coincides with the interval of the Calcite Sea II, suggesting that the Late Cretaceous pearl peak reflects a strong preservational bias linked to the proliferation of thick-shelled, calcitic bivalves, particularly inoceramids.

Overall, our understanding of pearl formation and the identity of pearl-producing bivalves in the geological past is strongly shaped by selective preservation. Because of the abundance of organic matter in pearls, they are poorly preserved in the fossil record. Pearls composed predominantly of calcite, produced by bivalves with thick calcitic shells, have a substantially higher preservation potential than aragonitic pearls. As a result, the fossil record of pearls is strongly biased towards calcitic producers.

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